

A REVISION OF THE FAMILY SQUILLIDAE (CRUSTACEA, STOMATOPODA), WITH THE DESCRIPTION OF EIGHT NEW GENERA

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ABSTRACT

The single Recent stomatopod crustacean family Squillidae is revised on the basis of characters afforded by the maxillipeds and telsons of both larvae and adults. Four families are recognized: Squillidae Latreille, 1803; Lysiosquillidae Giesbrecht, 1910; Gonodactylidae Giesbrecht, 1910; and Bathysquillidae Manning, 1967. Eight new genera based on species formerly assigned to *Squilla* are recognized. Two genera are removed from the synonymy of *Squilla*. Diagnostic features are illustrated and keys to genera of each family are presented.

INTRODUCTION

All Recent Stomatopoda traditionally have been assigned to the single family Squillidae. It has only been within the past five years that students of adult stomatopods have begun to realize that genera assigned to the family were conglomerates of unrelated species and that the family itself comprised several distinct groups of genera.

As noted in Manning (1963), Kemp (1913), in his monumental work on Indo-West Pacific stomatopods, recognized only six genera: *Squilla* Fabricius, 1787; *Gonodactylus* Berthold, 1827; *Lysiosquilla* Dana, 1852; *Pseudosquilla* Dana, 1852; *Coronida* Brooks, 1886; and *Odontodactylus* Bigelow, 1893. In 1921, Kemp & Chopra recognized *Hemisquilla* Hansen, 1895, which had been overlooked by Kemp in 1913. In 1926, Hansen erected *Coronidopsis*. The next genus to be proposed was *Parasquilla* Manning, 1961. Serène (1962) established two additional genera from the *Pseudosquilla* complex, *Manningia* and *Pseudosquillopsis*. In 1963, Manning recognized six new genera to include species formerly referred to *Pseudosquilla* and *Lysiosquilla*: *Eurysquilla* and *Eurysquilloides* from the *Pseudosquilla* complex, and *Nannosquilla*, *Acanthosquilla*, *Heterosquilla*, and *Bathysquilla* from the *Lysiosquilla* complex. He also resurrected *Coronis* from the synonymy of *Lysiosquilla*. Holthuis (1964) recognized *Harpiosquilla* from the *Squilla* section of the family, and *Hoplosquilla* from the *Gonodactylus* section. In 1966, Manning proposed the genus *Hadrosquilla*, and in 1967, he proposed the genus *Platysquilla* for species previously assigned to *Heterosquilla*. Holthuis & Manning (in press) recognized the following genera which had previously been syn-

onymized with others: *Clorida* Eydoux & Souleyet, 1842; *Leptosquilla* Miers, 1880; *Mesacturus* Miers, 1880; and *Protosquilla* Brooks, 1886.

At the time of the present writing, twenty-seven genera had been recognized, with most of the old genera other than *Squilla* subdivided to a greater or lesser extent. An additional ten genera are recognized herein.

A development parallel to the recognition of new genera has been the realization that these genera represent several distinct stocks or lines of evolution within the order. This is not a new idea, for subfamilies of the Squillidae had been proposed as early as 1910 by Giesbrecht, based largely on larval forms. Giesbrecht's ideas had gained some favor with those working with stomatopod larvae but had largely been ignored by those working with the adults. Serène (1962), in his study of *Pseudosquilla*, not only noted that *Squilla* needed to be studied in greater detail, but suggested that erection of several families would help to clarify the classification of the family. Manning (1963) pointed out that *Pseudosquilla*, *Lysiosquilla*, and *Bathysquilla* each represented distinct subgroups within the family, which, except for *Bathysquilla*, corresponded to the subdivision of the family proposed by Giesbrecht. Thus, for the first time, evidence derived from two separate sources, the study of larvae and the independent study of adults, supported a revision at the family level.

The increase in number of genera has been accompanied by an increase in the number of species. In 1913, Kemp listed 126 species then known to him. In 1951, Chace noted that 178 species had been described, and more than 50 species have been described or removed from synonymy since then. The genus *Squilla* (s. l.) now contains in excess of 106 species, and more than 230 species have been described in all genera.

Carcinologists have not revised the stomatopod genera for several reasons. Few students of the group have been familiar with all of the known species in any genus. Kemp (1913), who made the single largest contribution to our knowledge of the group, was almost totally unfamiliar with the Atlanto-East Pacific species. Most students of stomatopods have confined their systematic studies to limited geographic areas. Only two monographs based on material from worldwide areas have been published (Miers, 1880; Bigelow, 1894), and both of these studies were made before most of the species now known had been described. Many species are known from only one or two specimens and, because of their rarity in collections, are unavailable to most workers.

The understanding of true relationships within the group has been obscured, to some extent at least, by convergence of characters. The presence of longitudinal carinae on the body has been accepted as a characteristic of the genus *Squilla*, and carinate species have been assigned to that genus. Thus *Squilla ferussacii* (now *Parasquilla*) with its carinate abdomen and *Pseudosquilla*-like telson has been placed alternately in

Squilla and *Pseudosquilla*. Manning (1963) has shown that *Parasquilla* is not closely related to *Squilla* but shares many features with members of the genera *Pseudosquilla* and *Pseudosquillopsis*.

Retention of larval characters by adults and their parallel retention in different evolutionary lines has also tended to obscure relationships. Manning (1962) pointed out that the following features were characteristic of the postlarvae of *Alima hyalina*: (1) lack of anterolateral spines on the carapace; (2) reduction of abdominal carination; and (3) presence of movable apices on the submedian marginal teeth of the telson. All of these features are shared by the members of the genus *Meiosquilla*, proposed below. Some of these traits also appear in the Indo-West Pacific *Anchisquilla*, but the species of the latter do not appear to be closely related to those herein assigned to *Meiosquilla*.

In 1963, I briefly reviewed some of the earlier concepts of relationships of the stomatopods, including the apparently mutually exclusive schemes of Brooks (1886) and Kemp (1913) based on adults, and those of Hansen (1895), Giesbrecht (1910), Foxon (1932, 1939) and Gurney (1937, 1946) based on larval forms. It was pointed out that Hansen and Giesbrecht both arrived at similar groupings of the larval forms. Hansen utilized the shape of the last 3 maxillipeds, and Giesbrecht based his ideas on the type of larva (characterized by telson morphology, among other things). My preliminary analysis of adult morphology of *Pseudosquilla* and *Lysiosquilla* supported such an arrangement. Subsequent study of adult stomatopods with particular reference to maxilliped shape and telson structure, including the presence or absence of the median carina and the nature of the marginal denticles, completely substantiates the premise that there are four distinct groups of genera within the family Squillidae as currently recognized. These four groups of genera have been recognized by Manning (1967) as four families, Squillidae s.s., Lysiosquillidae Giesbrecht, Gonodactylidae Giesbrecht, and Bathysquillidae Manning. Members of these four families are distinct as larvae and as adults. At the present time our knowledge of fossil forms is so inadequate that, based on it, no postulates as to the origins and past relationships of the Recent stomatopods can be made. The fossil family Sculdidae is included in the key to families presented below, but will not be discussed further. A complete account of that family can be found in Holthuis & Manning (in press).

The present subdivision of the family is based in part on the structure of the last three maxillipeds and in part on the morphology of the telson. In the family Lysiosquillidae, the last three maxillipeds are broader than long, with the ventral margin of the propodi of the third and fourth maxillipeds beaded or ribbed (Fig. 2, a-c), and the telson lacks a sharp

dorsal carina (Fig. 1, a). The other three families all have slender third to fifth maxillipeds (Fig. 2, d-i) and the telson is provided with a sharp dorsal carina. The family Bathysquillidae has all marginal teeth of the telson provided with movable apices (Fig. 1, b), whereas the families Squillidae and Gonodactylidae have, at most, the submedian teeth provided with movable apices. These latter two families can be distinguished by the number of intermediate denticles on the telson, for in the Squillidae there are always more than four, whereas in the Gonodactylidae there are only two.

The recognition of families based on characters of adult stomatopods is supported by what is known about the larvae. The larval forms of the Lysiosquillidae hatch as antizoeae, with biramous thoracic appendages, and the pleopods appear in succession from front to rear; the known larvae all have broad maxillipeds. The larvae of the Squillidae and Gonodactylidae hatch as pseudozoeae, with two uniramous thoracic appendages and either four or five pleopods. Early larvae of the family Squillidae have but four pleopods, but later stages, known as alima larvae, have five pleopods and at least four intermediate denticles on the telson. Gonodactylid larvae develop into an erichthus stage, with no more than two intermediate denticles on the telson. In my opinion, these differences between stocks of larvae and their adults are fundamental, and very strongly support the recognition of four families within the Stomatopoda.

This account includes a brief characterization of each family, keys to the families and to the genera within each family, and a revision of the genera assigned herein to the Squillidae proper. Diagnostic sketches of the main family characters are provided, as are sketches illustrating features of members of the Squillidae. Genera occurring in the western Atlantic will be treated in greater detail in a revision of that fauna now in press. In general, illustrations provided herein have been made from Indo-West Pacific species, since all of the western Atlantic species will be illustrated in detail in that revision. Genera of the Lysiosquillidae and Gonodactylidae have been reviewed recently by Manning (1963) and Holthuis & Manning (in press) and, with the exception of changes in nomenclature subsequent to those papers, are not treated further here. An asterisk (*) next to a species name indicates that specimens of that species have been examined.

It was my intention to include in this paper lists of species for all genera not included by me in 1963. However, L. B. Holthuis is preparing an account of the Stomatopoda for the *Crustaceorum Catalogus* in which a complete synonymy will be presented for all species. In view of this, a list of the species in the Gonodactylidae would seem to be unnecessarily repetitive, inasmuch as all will be treated by him in that work.

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KEY TO THE FAMILIES OF STOMATOPODA

1. Exopod of uropods one-segmented, with movable spines on outer margin; fossil, Jurassic to Cretaceous *Sculdidae* Dames, 1886
- Exopods of uropods two-segmented, proximal only with movable spines; fossil and Recent 2
2. Telson lacking sharp median carina (Fig. 1, a); propodi of last 3 maxillipeds broad, beaded or ribbed ventrally (Fig. 2, a-c) *Lysiosquillidae* Giesbrecht, 1910
- Telson with sharp median carina; propodi of last 3 maxillipeds elongate, not beaded or ribbed ventrally (Fig. 2, d-i) 3
3. All marginal teeth of telson with movable apices (Fig. 1, b) *Bathysquillidae* Manning, 1967
- At most, submedian marginal teeth with movable apices 4
4. More than 4 intermediate denticles present on telson (Fig. 1, c) *Squillidae* Latreille, 1803
- No more than 2 intermediate denticles present on telson (Fig. 1, d) *Gonodactylidae* Giesbrecht, 1910

Family *Lysiosquillidae* Giesbrecht, 1910

Erichthidae White, 1847: 82 (larva).

Lysiosquillinae Giesbrecht, 1910: 148.—Gurney, 1946: 134.—Manning, 1963: 324-325.

Lysiosquillidae Manning, 1967: 238 (key).

Definition.—Propodi of third and fourth thoracic appendages as broad as or broader than long and beaded ventrally (Fig. 2, a-c), propodus of fourth almost twice as broad as that of fifth appendage; telson (Fig. 1, a) without distinct median carina, number of marginal teeth variable; submedian teeth of telson usually movable, submedian denticles present.

Type-genus.—*Lysiosquilla* Dana, 1852.

Number of genera.—Nine, distinguished in key below.

Remarks.—The genus *Erichthys* Latreille, 1817, the type-genus of *Erichthidae* White, was suppressed by the International Commission on Zoological Nomenclature in order to preserve the well-known *Lysiosquilla*

Dana. This action validated *Lysiosquillinae* Giesbrecht, 1910, which was raised to family rank by Manning (1967).

Although no categories above the generic level were recognized by me in my preliminary review of *Pseudosquilla* and *Lysiosquilla* (1963), I pointed out that the genera of the "Lysiosquilla complex" were very closely related and might require recognition at the family level. The heterogeneity of *Heterosquilla* was also pointed out. The only major changes in the alignment of genera of the "Lysiosquilla complex" since 1963 have resulted from more detailed study of the species then assigned to *Heterosquilla*. Two genera which have been recognized for two groups of species originally placed in *Heterosquilla* are listed below, and a third new genus, *Platysquilla*, was recognized by Manning (1967). The remaining species in *Heterosquilla* fall into two subgenera, described by me in 1966, and appear to be homogeneous.

KEY TO THE GENERA OF THE FAMILY LYSIOSQUILLIDAE

1. Distal segment of endopod of first 2 walking legs elongate; proximal portion of outer margin of uropodal endopod at most angled inward, not folded 2
Distal segment of endopod of first 2 walking legs ovate or subcircular; proximal portion of outer margin of uropodal endopod folded 4
2. Dactylus of raptorial claw inflated basally; propodus of claw pectinate proximally only; rostral plate rounded or subrectangular *Coronida* Brooks, 1886
Dactylus of raptorial claw not inflated basally; propodus fully pectinate; rostral plate cordiform or triangular 3
3. Median dorsal surface of telson with at most a low triangular boss; movable submedian teeth rarely present; marginal teeth of telson usually fused *Lysiosquilla* Dana, 1852
Median dorsal surface of telson with raised median projection, lobed or spined posteriorly; movable submedian marginal teeth of telson always present, remainder of teeth and denticles distinct, not fused *Heterosquilla* Manning, 1963
4. Dorsal surface of telson with fan-shaped series of 5 or more spines *Acanthosquilla* Manning, 1963
Dorsal surface of telson unarmed or with at most a single median projection 5
5. Posterior margin of dorsal surface of telson produced into false eave overhanging true posterior armature 6
Posterior margin of dorsal surface of telson with single median projection, not produced into false eave 7
6. Antennal protopod with papillae; 5 epipods present; spines on

uropodal exopod not spatulate	<i>Hadrosquilla</i> Manning, 1966
Antennal protopod without papillae; 4 epipods present; spines on uropodal exopod spatulate	<i>Nannosquilla</i> Manning, 1963
7. Mandibular palp present; telson with 1 pair of fixed marginal teeth	<i>Coronis</i> Desmarest, 1823
Mandibular palp absent; telson with more than 1 pair of fixed marginal teeth	8
8. Telson with 4 pairs of fixed marginal teeth; inferodistal angle of ischium of raptorial claw unarmed	<i>Platysquilla</i> Manning, 1967
Telson with 2 pairs of fixed marginal teeth; inferodistal angle of ischium of claw with strong spine	<i>Austrosquilla</i> Manning, 1966

Hadrosquilla Manning, 1966

Hadrosquilla Manning, 1966: 115.

Diagnosis.—Manning, 1966: 115.

Remarks.—*Hadrosquilla* includes only the following species:

1. **Lysiosquilla perpasta* Hale, 1924

Range.—Australia and Tasmania.

Austrosquilla Manning, 1966

Heterosquilla (*Austrosquilla*) Manning, 1966: 127.

Diagnosis.—Manning, 1966: 127.

Remarks.—*Austrosquilla*, originally erected as a subgenus of *Heterosquilla*, is recognized as a genus, herein. It contains the following species:

1. **Lysiosquilla osculans* Hale, 1924
2. **Lysiosquilla vercoi* Hale, 1924

Range.—Australia and Tasmania.

Type-species.—*Lysiosquilla vercoi* Hale, by original designation.

Platysquilla Manning, 1967

Platysquilla Manning, 1967: 238.

Diagnosis.—Body smooth, depressed; eye of moderate size, cornea faintly bilobed; rostral plate quadrate, with apical spine; carapace lacking carinae or spines, cervical groove indicated on lateral plates only; antennal protopod with mesial and ventral papillae; dactylus of raptorial claw with 9 or more teeth; propodus of claw fully pectinate; mandibular palp absent; at least 4 epipods present; thoracic and abdominal somites lacking longitudinal carinae; telson broad, with obtuse, median, posterior projection; posterior armature of telson consisting of, on either side of midline, 1 movable submedian tooth and 4 fixed teeth, with a denticle between the

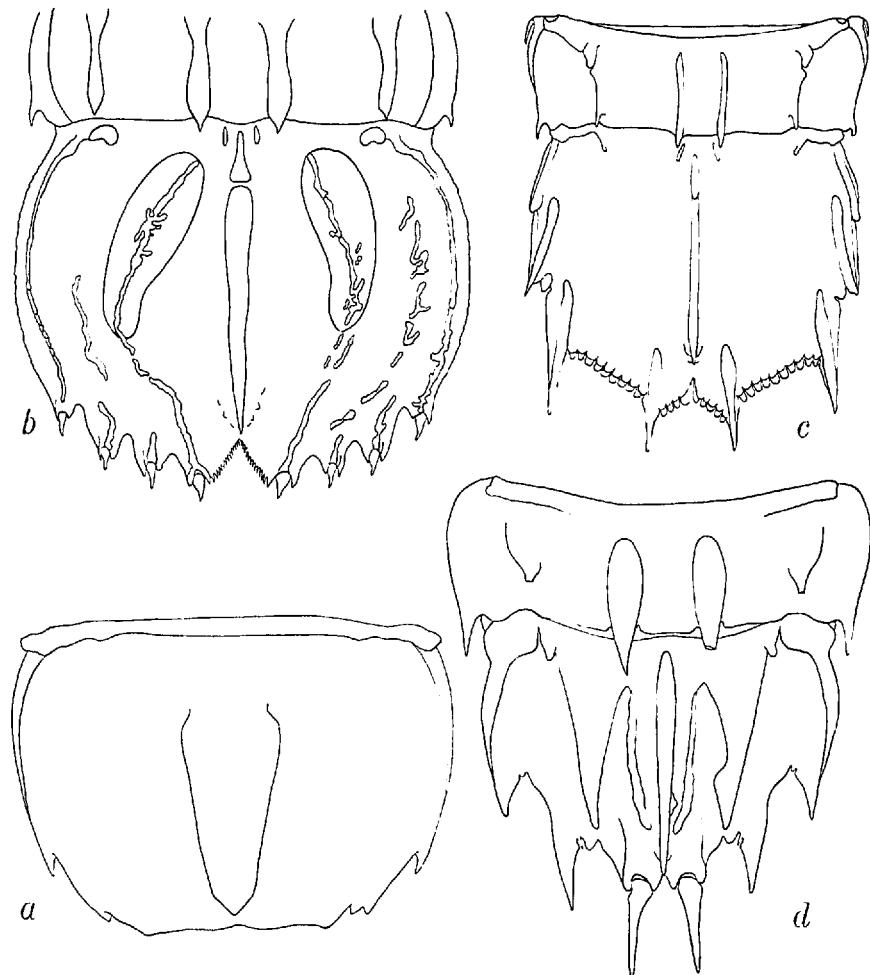


FIGURE 1. Outline of telson of: *a*, *Lysiosquilla maculata* (Fabricius); *b*, *Bathysquilla microps* (Manning); *c*, *Oratosquilla oratoria* (de Haan); *d*, *Pseudosquilla ciliata* (Fabricius).

consecutive members of the latter set; inner spine of basal prolongation the longer; size moderate, TL 75 mm or less.

Remarks.—*Platysquilla* contains two species:

1. **Squilla eusebia* Risso, 1816
2. **Lysiosquilla enodis* Manning, 1962

The four pairs of fixed marginal teeth on the telson distinguish *Platysquilla* from all other genera in the family.

Range.—Atlantic.

Type-species.—*Squilla eusebia* Risso, 1816, by original designation.

Gender.—Feminine.

Family Bathysquillidae Manning, 1967

Bathysquillidae Manning, 1967: 238.

Definition.—Propodi of last 3 maxillipeds longer than broad, propodus of fourth not markedly broader than that of fifth appendage; telson (Fig. 1, b) with median dorsal carina and 4 pairs of marginal teeth, all with movable apices; submedian denticles present, all other denticles absent.

Type-genus.—*Bathysquilla* Manning, 1963.

Number of genera.—One.

Remarks.—Manning (1963) noted that the genus *Bathysquilla*, which includes but two species, showed no close affinities with any of the other genera then placed in the Squillidae. The family Bathysquillidae is felt to be sufficiently distinct from the three subfamilies distinguished by Giesbrecht (1910) to warrant separation at this level.

The sharp median carina on the telson immediately distinguishes *Bathysquilla* from all genera included in the Lysiosquillidae, and the lack of intermediate denticles on the telson excludes the genus from the Gondactylidae and Squillidae. The structure of the telson is unique in *Bathysquilla*, for in no other genus are all of the marginal teeth of the telson provided with movable apices.

Larval forms have not been identified for *Bathysquilla*. However, among the stomatopods collected by the GALATHEA there is a late larva which is clearly a *Bathysquilla* and which is unique among stomatopod larvae in several features. It will be described in a report on the GALATHEA stomatopods now in preparation.

Family Squillidae Latreille, 1803

Squillares Latreille, 1803: 36.

Squillidae White, 1847: 83 (correction of *Squillares*).—Manning, 1967: 238 (key).—Holthuis & Manning, in press.

Definition.—Propodi of third and fourth thoracic appendages as long as or longer than broad (Fig. 2, d-f), lacking ventral ribbing; telson (Fig. 1, c) with distinct median carina, at most submedian marginal teeth with movable apices; submedian denticles always present; more than 4 intermediate denticles present.

Type-genus.—*Squilla* Fabricius, 1787.

Number of genera.—Fourteen, as distinguished below.

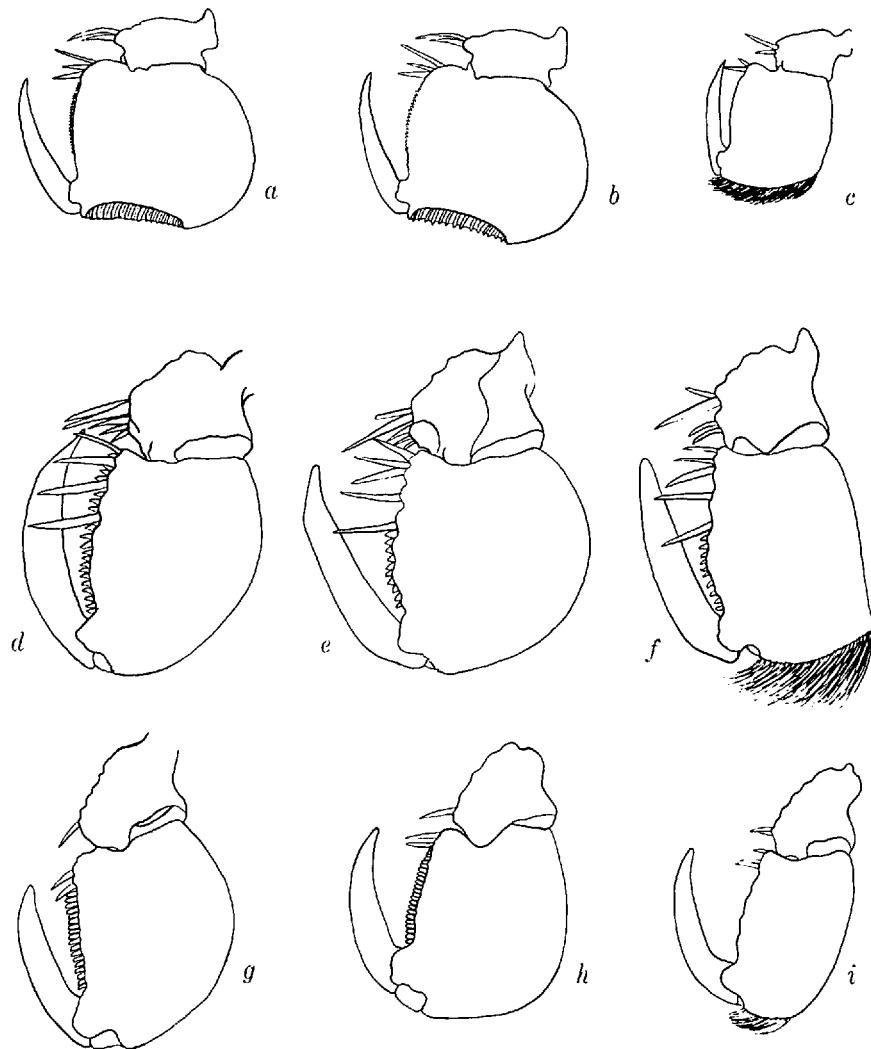


FIGURE 2. Outline of third, fourth, and fifth maxillipeds of: a-c, *Lysiosquilla maculata* (Fabricius); d-f, *Oratosquilla oratoria* (de Haan); g-i, *Pseudosquilla ciliata* (Fabricius).

Remarks.—Even with the recent recognition of *Harpiosquilla* Holthuis, *Leptosquilla* Miers, and *Clorida* Eydoux & Souleyet by Holthuis & Manning (in press) and the present recognition of *Alima* Leach and *Pterygosquilla* Hilgendorf, the genus *Squilla* Fabricius is a conglomerate of 79 species

comprising several recognizable species-groups. The present account of the family Squillidae includes a definitive revision of the genus *Squilla* in which eight new genera are proposed, and a total of 14 genera are recognized.

That several distinct groups of species occur within the genus *Squilla* has been recognized by all serious students of the stomatopods. Kemp (1913) noted that the species then included in the genus fell into two broad sections based upon the structure of the lateral process of the fifth thoracic somite. More recently, Serène (1962), in a revision of *Pseudosquilla*, pointed out that *Squilla* could be divided into at least five groups.

Kemp's (1913) subdivision of the genus into two broad sections, as noted above, was based on the form of the lateral process of the fifth thoracic somite, whether bifurcated (Fig. 7, c, e) or simple (Fig. 7, a). In the section which includes most of the Indo-West Pacific species, the lateral process is made up of two lobes, an anteriorly curved anterior spine and a blunter posterior lobe; species included in that section, in general, lack the ventral spines on that somite. In the other section, comprising mainly Atlanto-East Pacific species, the lateral process is produced into a single spine, and ventral spines are also present.

These differences are the result of the ventral rotation of the anterior spine in relation to the posterior. This is clearly seen when the lateral processes of *Alima hyalina* (Fig. 7, e-f) and *Oratosquilla oratoria* (Fig. 7, c-d) are compared with the lateral process of *Squilla empusa* (Fig. 7, a-b). In *A. hyalina*, both lobes of the lateral process are on the same longitudinal plane; in *O. oratoria* and its allies, although both lobes appear to comprise a bilobed process in dorsal view, the anterior lobe is actually situated slightly ventral to the posterior. In *S. empusa*, the anterior spine is on the ventral surface, and the posterior spine alone makes up the lateral process of the somite.

In my opinion, these differences are fundamental, and represent the morphological divergence of two stocks of species within the family.

The current study indicates that there are four distinct groups of genera within the old genus *Squilla*. The first group includes but one genus, *Harpiosquilla* Holthuis, characterized by the presence of erect spines on the propodus of the raptorial claw (Fig. 3, a) and a deep posterolateral excavation on the carapace. This genus occupies an isolated position in the family and does not appear to be closely related to any of the other genera. In all of the remaining groups of genera, the propodus is pectinate (Fig. 3, b) rather than armed with erect spines and the posterolateral margin of the carapace is entire.

The second group of genera is characterized by the presence of a bifurcate lateral process on the fifth thoracic somite (Fig. 7, c-f). This group, comprising five genera, includes *Squilla oratoria* de Haan and its

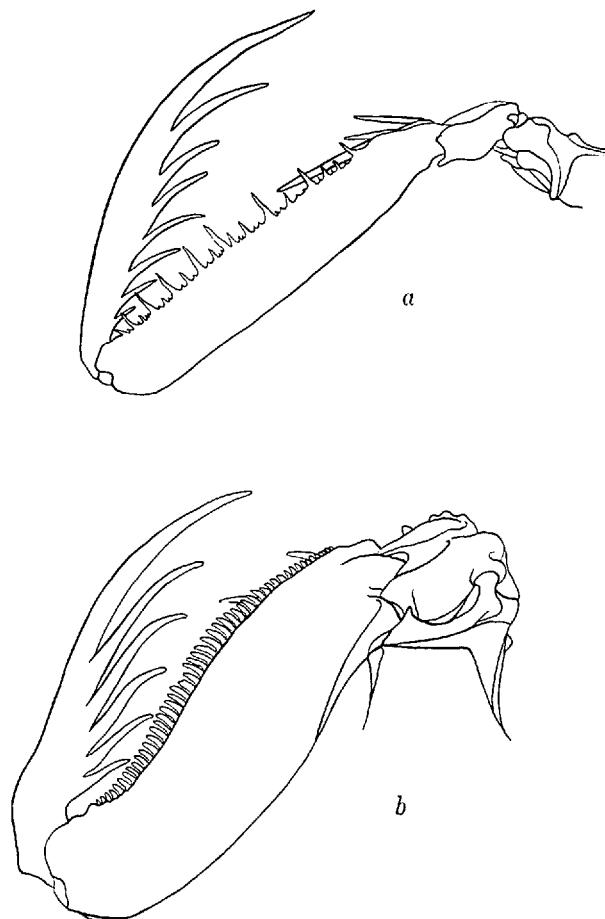


FIGURE 3. Outline of raptorial claw of: *a*, *Harpiosquilla harpax* (de Haan); *b*, *Oratosquilla oratoria* (de Haan).

relatives. The genera are largely found in the Indo-West Pacific, as noted by Kemp, with the exception of *Alima* Leach, which includes two Atlantic species.

The third and fourth groups of genera both have the lateral process of the fifth thoracic somite produced into a single spine; they differ primarily in eye size, body shape, and carination. The third group includes those genera related to the small-eyed *Clorida*, in which the eye is very small, the carapace has a reduced complement of carinae, and the inflated body also has its carination reduced. Many of the genera related to *Clorida* also

have the submedian marginal teeth of the telson provided with movable apices; this feature, in the Squillidae s.s., is found only in those genera related to *Clorida*. Although *Clorida* occurs only in the Indo-West Pacific, related genera are found in the Atlantic and East Pacific. The fourth group of genera includes only *Squilla*, in its restricted sense, characterized by large eyes and well-developed carination of the carapace and body. *Squilla*, as defined herein, occurs only in the Atlanto-East Pacific.

Kemp (1913), and later Kemp & Chopra (1921), examined other characters, including the shape of the eye, the presence or absence of a mandibular palp, and the number of epipods. These authors concluded, after considering the genus *Squilla* as a whole, that the palp and epipods may be of value at the specific level but could not be used as a character to show affinities at the generic level. To some extent this is true. These characters, however, if used in combination with others, including the shape and armature of the claw, the reduction of carination of the carapace and abdomen, the general facies of the abdomen and telson, and the structure of the uropod, can be very helpful in delimiting groups of species.

Consider, for example, the epipods. The maximum number now found in stomatopods is five, one at the base of each of the maxillipeds. In some species, particularly those related to *Squilla mantis* (*Squilla* s.s.), there are usually five epipods present; in other species the number is reduced. In the species group with the *oratoria* facies, the basic number is four, a reduction of one throughout the group. In some species of that group the reduction is carried even further, but the reduction must be considered in relation to the condition existing in related species, not species of other genera. In another group including the American *S. dubia* and the Indo-West Pacific *S. scorpio* and their allies, the basic number seems to be two, rather than four or five; one species, *S. dubia*, has three epipods. In this group, which is recognized below as a new genus, reduction in epipods is a basic feature. The epipods, when considered alone, do not provide any clear clues to relationships; when considered in combination with other characters, they do provide additional data that are most helpful.

The same can be said for the structure of the eyes. Eye shape, including the relation of the stalk to the cornea, the shape of the stalk or the cornea, and the angle at which the cornea is placed upon the stalk, can be used as a reliable guide to relationships, if it is kept in mind that although eye shape may be very characteristic for one genus, the independent acquisition of a similar eye shape can occur in other genera, and value of eye shape must be assessed in relation to other features. Thus the genus *Clorida*, as recognized herein, is made up of species with small eyes, in which the stalk is dilated and the cornea is very small, often being narrower than the stalk. This same feature, however, is found in combination with other characteristics in some species of *Cloridopsis*, a new genus which

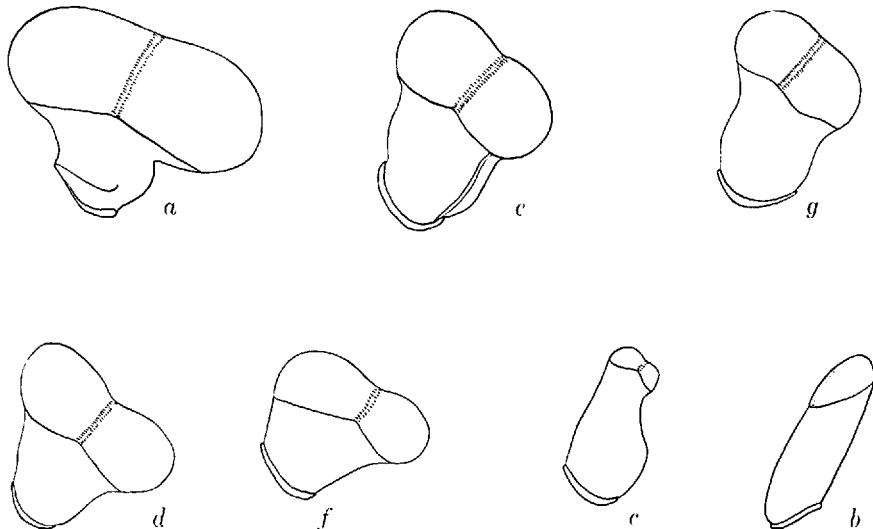


FIGURE 4. Outline of eyes of: *a*, *Harpiosquilla* sp.; *b*, *Leptosquilla schmeltzii* (A. Milne-Edwards) (from Kemp, 1913); *c*, *Clorida microphthalmalma* (H. Milne-Edwards); *d*, *Meiosquilla desmarestii* (Risso); *e*, *Anchisquilla fasciata* (de Haan); *f*, *Anchisquilla miles* (Hess); *g*, *Cloridopsis scorpio* (Latreille).

includes *Squilla scorpio*, *S. dubia* and their allies, as well as in *Squilla foveolata*, an Indo-West Pacific species allied to *Squilla oratoria*, placed herein in a new monotypic genus. The independent occurrence of these features in other groups does not minimize its importance in *Clorida*.

The present study lends support to Kemp's observations on the importance of the structure of the lateral process of the fifth thoracic somite. It also indicates that the presence of movable apices on the submedian teeth of the telson, found only in certain groups of species, is equally important. Within the family Squillidae *s.s.* these movable apices occur only in the small-eyed genera related to *Clorida*. There is no evidence at this time that this character has been acquired or lost independently in related species. It occurs in *Clorida*, *Leptosquilla*, *Pterygosquilla*, *Meiosquilla*, and *Anchisquilla*; it is absent in *Cloridopsis*, *Squilloides*, *Squilla* *s.s.*, *Harpiosquilla*, as well as the groups of genera related to *Squilla oratoria*.

The presence or absence of inner spines on the basal prolongation of the uropod and the structure of the lateral processes of the sixth and seventh thoracic somites, are not stressed in this revision of *Squilla*. These characters may well prove to be of some importance in classification at the generic level. Reluctance to establish several monotypic genera has

led me to group several similar but possibly unrelated species together in *Anchisquilla*; this assemblage of species is discussed below in the account of the genus.

Among those species with movable apices on the submedian teeth of the telson, the inner margin of the basal prolongation of the uropod is provided with spines in *Clorida*, *Leptosquilla*, seven species of *Meiosquilla*, and three of the species of *Anchisquilla*; in all of these the lateral processes of the sixth and seventh thoracic somites are rounded, not bilobed. The basal prolongation is also armed in *Squilloides*, in *Carinosquilla* (one of the genera related to *S. oratoria*), and in one American species of *Squilla*, *S. rugosa* Bigelow, and the lateral processes of the sixth and seventh thoracic somites are simple, not bilobed. In species of *Squilla* in which the basal prolongation is armed, notably *S. rugosa*, the lateral processes of the sixth and seventh thoracic somites are not bilobed. It seems possible that the presence of spines on the basal prolongation of the uropod is more important at the generic level in some of the Indo-West Pacific groups than in *Squilla*. Those species of *Squilla* in which this feature occurs are otherwise very similar in basic facies, as can readily be seen by a comparison of *S. hancocki* Schmitt with *S. tiburonensis* Schmitt or *Squilla rugosa*. Furthermore, in *Squilla*, the presence of spines on the basal prolongation of the uropod is accompanied by formation of dorsal tubercles on the telson.

That features characteristic of one genus may occur independently in unrelated genera is demonstrated by the occurrence of body carinae (one of the characteristics of *Squilla* Fabricius and other genera in the Squillidae) in *Parasquilla* Manning, now in the Gonodactylidae. One of the characteristic features of *Leptosquilla* Miers (Squillidae), the elongate antennular somite, occurs also in *Eurysquilloides* Manning (Gonodactylidae). Finally, the erect spines on the propodus of the raptorial claw have developed in two different, distantly related genera, *Bathysquilla* Manning (Bathysquillidae) and *Harpiosquilla* Holthuis (Squillidae).

The key to the genera given below is artificial, and groupings within the key are not intended to imply relationships.

The statement that the carapace has a normal complement of carinae refers to the condition in *Squilla*, where median, intermediate, lateral, and marginal carinae are present. Similarly, the normal complement of carinae on the abdomen refers to the condition found in *Squilla* where four pairs of carinae are present: submedian, intermediate, lateral, and marginal. These complements of carinae may be augmented by additional carinae, or may be modified by suppression of one or more of them. Carinal terminology for squillids has been illustrated by Kemp (1913) and Holthuis & Manning (in press).

KEY TO THE GENERA OF THE FAMILY SQUILLIDAE

1. Propodus of raptorial claw with erect spines; posterolateral margin of carapace with deep excavation ... *Harpiosquilla* Holthuis, 1964
- Propodus of claw pectinate, without erect spines; posterolateral margins of carapace entire 2
2. Lateral process of fifth thoracic somite a single spine or lobe 3
- Lateral process of fifth thoracic somite bilobed 10
3. Submedian teeth of telson with movable apices 4
- Submedian teeth of telson with fixed apices 8
4. Antennular somite greatly elongated, rostral plate not extending to midlength; cornea subglobular *Leptosquilla* Miers, 1880
- Antennular somite not elongated, rostral plate extending beyond midlength; cornea flattened or bilobed 5
5. Ocular scales each produced into an erect spine; sub-Antarctic *Pterygosquilla* Hilgendorf, 1890
- Ocular scales rounded or subtruncate, never produced into erect spines; tropical or temperate 6
6. Eyes very small, stalk usually inflated, cornea rarely broader than stalk; ocular scales fused *Clorida* Eydoux & Souleyet, 1842
- Eyes small or of moderate size, stalk not inflated, cornea always broader than stalk; ocular scales separate 7
7. Telson lacking prelateral lobes; first to fifth abdominal somites without submedian carinae *Meiosquilla*, new genus
- Prelateral lobes of telson usually present; if absent, submedian carinae present on first five abdominal somites *Anchisquilla*, new genus
8. No more than 3 epipods present *Cloridopsis*, new genus
- 4 or 5 epipods present 9
9. Carapace with full complement of carinae; inner margin of basal prolongation of uropod usually serrate, if spined, telson with dorsal tubercles *Squilla* Fabricius, 1787
- Carapace usually with reduced complement of carinae (if complete, palp absent); inner margin of basal prolongation of uropod with spines; telson without dorsal tubercles *Squilloides*, new genus
10. Lateral processes of sixth and seventh thoracic somites bilobed 11
- Lateral processes of sixth and seventh thoracic somites not bilobed *Alima* Leach, 1817
11. Eye small, stalk inflated, much broader than cornea; body covered with raised carinae forming mesh-like reticulations *Dictyosquilla*, new genus
- Eye large, stalk not inflated, cornea broader than stalk; body not covered with carinae forming mesh-like reticulations 12

12. Abdomen with numerous longitudinal carinae, more than 8 13
 Abdomen with no more than 8 longitudinal carinae
 *Oratosquilla*, new genus

13. Carapace with more than 7 longitudinal carinae
 *Carinosquilla*, new genus
 Carapace with no more than 7 longitudinal carinae
 *Lophosquilla*, new genus

Harpiosquilla Holthuis, 1964

Harpiosquilla Holthuis, 1964: 140.—Holthuis & Manning, in press (with an account of the genus).

Diagnosis.—Eye large, T-shaped, cornea bilobed and distinctly broader than stalk (Fig. 4, a); ocular scales separate; carapace with reduced carinae, with deep posterolateral excavations; mandibular palp present; 5 epipods present; dactylus of raptorial claw with teeth, upper margin of propodus with series of spaced, erect spines (Fig. 3, a); lateral process of fifth thoracic somite an inconspicuous lobe, lateral processes of next 2 somites not strongly bilobed, margins sinuous; abdomen broad, submedian carinae poorly marked or absent; telson without supplementary dorsal ornamentation, submedian teeth with fixed apices, prelateral lobes present; inner margin of basal prolongation of uropod serrate.

Remarks.—*Harpiosquilla* includes but three species:

1. **Squilla raphidea* Fabricius, 1798
2. **Squilla harpax* de Haan, 1844
3. **Squilla annandalei* Kemp, 1911

The erect spines on the propodus of the raptorial claw (Fig. 3, a) and the deep posterolateral excavations of the carapace will serve to distinguish *Harpiosquilla* from all other genera of the Squillidae s.s. The erect spines on the propodus are also characteristic of *Bathysquilla* Manning, a distantly related genus. The affinities of *Harpiosquilla* within the Squillidae are unknown.

Range.—Indo-West Pacific.

Type-species.—*Squilla harpax* de Haan, 1844, by original designation.

Leptosquilla Miers, 1880

Leptosquilla Miers, 1880: 12.—Holthuis & Manning, in press.

Diagnosis.—Eye small, cornea subglobular, scarcely expanded beyond outline of long stalk (Fig. 4, b); ocular scales fused in midline; antennular somite greatly elongated; carinae of carapace reduced, carapace rounded posterolaterally; mandibular palp absent; 4 epipods present; dactylus of

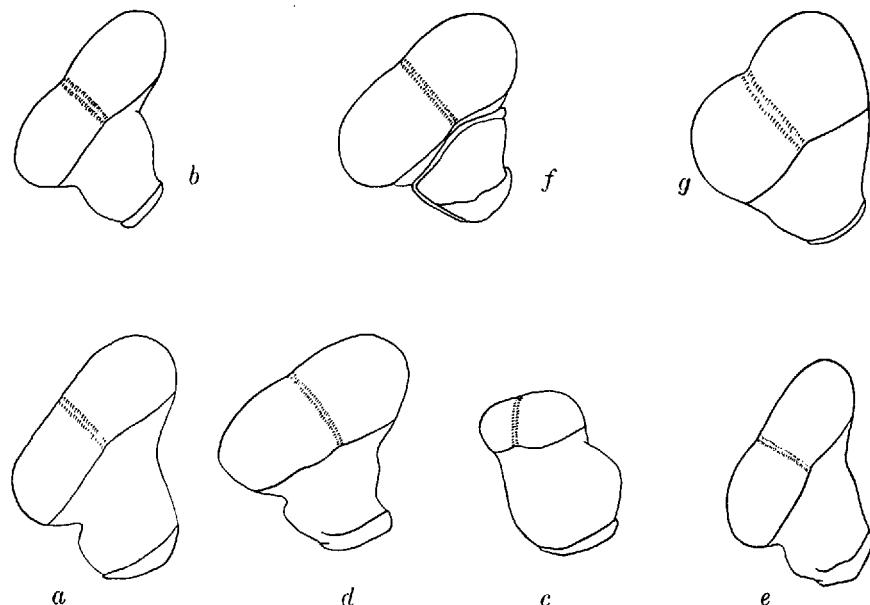


FIGURE 5. Outline of eyes of: *a*, *Squilla empusa* Say; *b*, *Squilloides leptosquilla* (Brooks); *c*, *Dictyosquilla joveolata* (Wood-Mason); *d*, *Lophosquilla costata* (de Haan); *e*, *Oratosquilla oratoria* (de Haan); *f*, *Carinosquilla multicarinata* (White); *g*, *Alima hyalina* Leach.

raptorial claw with 6-7 teeth, propodus with upper margin pectinate; lateral processes of fifth, sixth and seventh thoracic somites not bilobed, that of fifth somite a sharp spine; abdomen lacking submedian carinae on first 5 somites; telson broader than long, with 3 pairs of marginal teeth, submedians with movable apices; inner margin of basal prolongation of uropod with spines.

Remarks.—This genus includes but one species:

1. **Squilla schmeltzii* A. Milne-Edwards, 1873

Leptosquilla, which resembles *Clorida* in many features, can be distinguished from all other genera in the family Squillidae by the elongate antennular somite, a feature which it shares with *Euryxulloides*. There may be two species in the genus, for the specimens reported by Holthuis (1941) differ from those reported by Hansen (1926) in having two rounded lobes between the spines of the basal prolongation of the uropod.

Range.—Indo-West Pacific.

Type-species.—*Squilla schmeltzii* A. Milne-Edwards, 1873, by monotypy.

Pterygosquilla Hilgendorf, 1890

Pterygosquilla Hilgendorf, 1890: 172.

Diagnosis.—Eye of moderate size, cornea bilobed, noticeably broader than stalk; ocular scales produced into erect spines; carapace narrowed anteriorly, carinae reduced, posterolateral angles rounded; mandibular palp present; 4 epipods present; dactylus of raptorial claw with 6-10 teeth, propodus with upper margin pectinate; lateral process of fifth thoracic somite a single spine, lateral processes of next 2 somites each produced into posteriorly directed spine; abdomen convex, normal complement of carinae usually present; telson broad, smooth dorsally, submedian teeth with movable apices; prelateral lobes absent; inner spine of basal prolongation of uropod with erect spines on inner margin.

Remarks.—*Pterygosquilla* contains two species:

1. **Squilla armata* H. Milne-Edwards, 1837
2. **Squilla gracilipes* Miers, 1881

The ocular scales which are produced into erect spines will immediately distinguish members of this genus from all other squillids.

Range.—Sub-Antarctic, off Patagonia, South Africa, and New Zealand.

Type-species.—*Pterygosquilla laticauda* Hilgendorf, 1890, by monotypy. *P. laticauda* is a subjective junior synonym of *S. gracilipes* Miers.

Clorida Eydoux & Souleyet, 1842

Clorida Eydoux & Souleyet, 1842: 264.—Holthuis & Manning, in press (with other references).

Diagnosis.—Eye small, cornea bilobed, rarely broader than dilated stalk (Fig. 4, c); ocular scales fused medially; carapace strongly narrowed anteriorly, carinae reduced, posterolateral angles rounded; mandibular palp usually present; 2-4 epipods present (1 species with 2); dactylus of raptorial claw with 4-5 teeth, propodus with upper margin pectinate; lateral process of fifth thoracic somite a single spine or lobe, lateral processes of next 2 somites not bilobed; abdomen flattened, carinae usually reduced in number and poorly marked; telson broad, inflated, with dorsal spines or tubercles, submedian teeth with movable apices, prelateral lobes present or absent; basal prolongation of uropod with teeth on inner margin.

Remarks.—This genus contains 14 species:

1. **Squilla microphthalmia* H. Milne-Edwards, 1837
2. **Clorida latreillei* Eydoux & Souleyet, 1842
3. *Clorida decorata* Wood-Mason, 1875
4. **Chloridella depressa* Miers, 1880
5. **Chloridella rotundicauda* Miers, 1880
6. **Squilla chlorida* Brooks, 1886

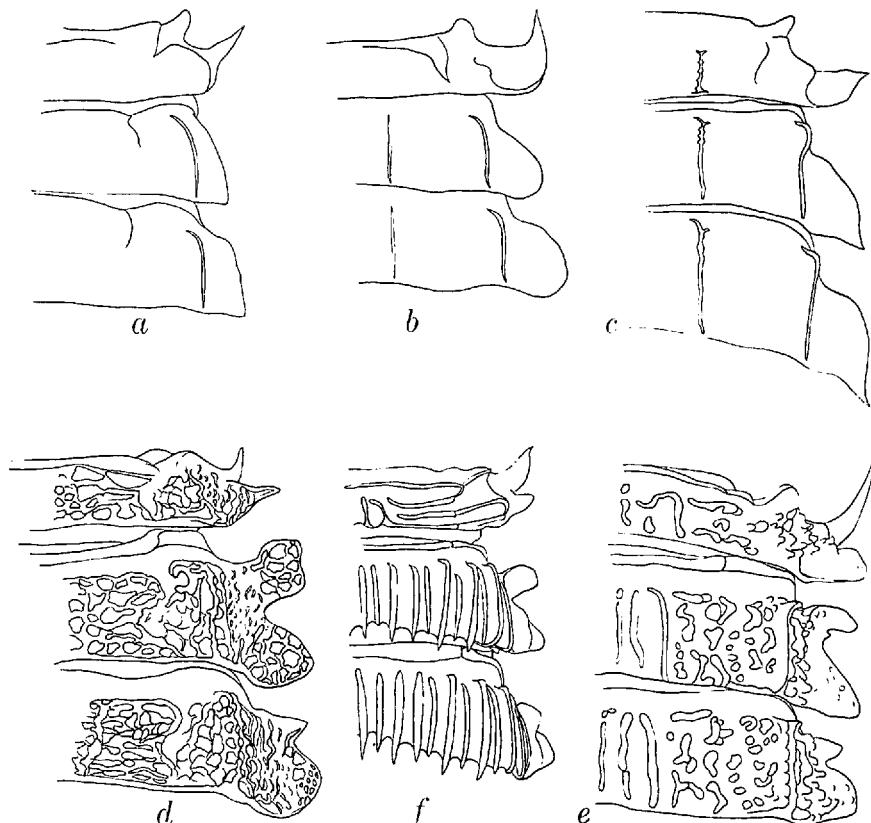


FIGURE 6. Lateral processes of fifth to seventh thoracic somites of: *a*, *Anchisquilla fasciata* (de Haan); *b*, *Cloridopsis scorpio* (Latreille); *c*, *Squilloides leptosquilla* (Brooks); *d*, *Dictyosquilla foveolata* (Wood-Mason); *e*, *Lophosquilla costata* (de Haan); *f*, *Carinosquilla multicarinata* (White).

7. **Squilla fallax* Bouvier, 1914
8. **Squilla ambigua* Hansen, 1926
9. **Squilla incerta* Hansen, 1926
10. **Squilla verrucosa* Hansen, 1926
11. **Squilla mauliana* Bigelow, 1931
12. **Squilla choprail* Tweedie, 1935
13. *Squilla merguiensis* Tiwari & Biswas, 1952
14. *Squilla granti* Stephenson, 1953

The small eyes, fused ocular scales, reduced carination of body and carapace, tuberculate telson with movable submedian teeth, and basal

prolongation of uropod with inner spines will serve to distinguish *Clorida*, which resembles both *Leptosquilla* and *Cloridopsis*. Members of the latter genus lack movable apices on the submedian teeth of the telson and the inner spines on the basal prolongation of the uropod.

Both *Squilla fallax* and *S. mauiana* may eventually prove to belong in other genera. *S. fallax* is placed here on the basis of its close resemblance to the other species, even though its eyes are not typically inflated; if Bouvier's (1915) figures are accurate, the ocular scales are fused. *S. mauiana* is the only species herein assigned to *Clorida* in which the number of epipods is reduced to two; as far as I can determine, all other species have four.

S. gibba Nobili, which was aligned with the small-eyed species by Kemp (1913), is tentatively assigned to *Cloridopsis*; it completely lacks the dorsal sculpture of the telson that is characteristic of the genus, as well as the spines on the inner margin of the basal prolongation of the uropod.

Range.—Indo-West Pacific.

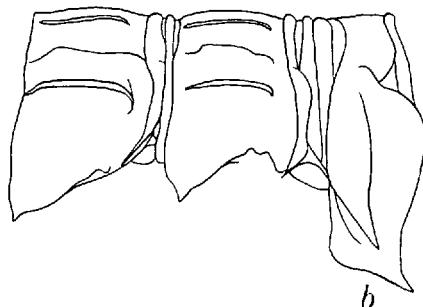
Type-species.—*Clorida latreillei* Eydoux & Souleyet, 1842, by subsequent designation by Fowler, 1912, p. 302.

Meiosquilla, new genus

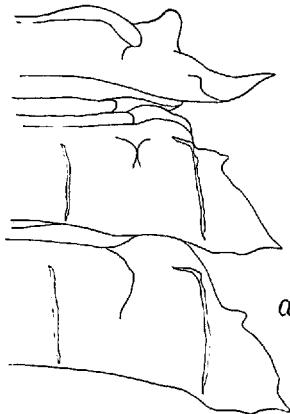
Diagnosis.—Eye large, cornea bilobed, noticeably broader than stalk (Fig. 4, d); ocular scales separate, truncate; carinae of carapace reduced, at most reflected marginals and posterior portion of intermediates present; mandibular palp absent; no more than 4 epipods present; dactylus of raptorial claw with 4-5 teeth, upper margin of propodus pectinate; lateral process of fifth thoracic somite single, often inconspicuous; lateral processes of next two somites each composed of a single lobe; last 3 thoracic and first 5 abdominal somites lacking submedian carinae; telson broad, dorsally carinate in some species, submedian teeth with movable apices (Fig. 8, a); prelateral lobes absent; inner spine of basal prolongation of uropod usually with spinules on inner margin (Fig. 9, a).

Remarks.—*Meiosquilla* includes the following species:

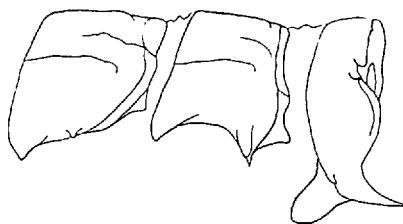
1. **Squilla desmarestii* Risso, 1816
2. **Squilla polita* Bigelow, 1891
3. **Squilla quadridens* Bigelow, 1893
4. **Squilla pallida* Giesbrecht, 1910
5. **Squilla swetti* Schmitt, 1940
6. **Squilla tricarinata* Holthuis, 1941
7. **Squilla oculinova* Glassell, 1942
8. **Alima lebouri* Gurney, 1946
9. **Squilla schmitti* Lemos de Castro, 1955
10. **Squilla randalli* Manning, 1962



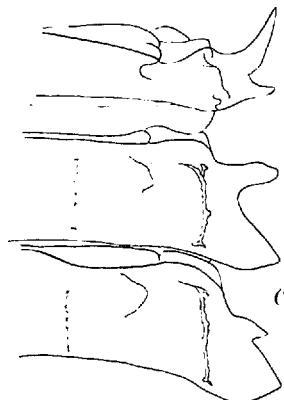
b



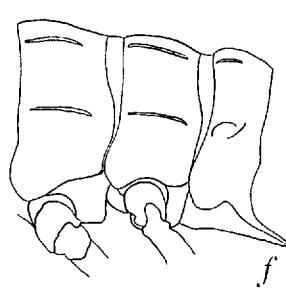
a



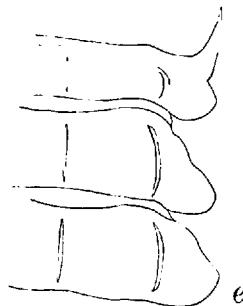
d



c



f



e

FIGURE 7. Lateral processes of fifth to seventh thoracic somites, in dorsal and lateral view, of: a-b, *Squilla empusa* Say; c-d, *Oratosquilla oratoria* (de Haan); e-f, *Alima hyalina* Leach.

The relatively small size (TL 100 mm or less), reduction in development of some features, including number of epipods and teeth on the raptorial claw and reduction of body carinae, and presence of movable apices on the submedian teeth of the telson will serve to distinguish members of this genus. Species of *Anchisquilla* and *Squilloides*, some of which are superficially similar to species of *Meiosquilla*, differ in one or more of these major features. In addition, all species of *Squilloides* have fixed apices on the submedian teeth of the telson.

Range.—Atlanto-East Pacific.

Type-species.—*Squilla quadridens* Bigelow, 1893.

Gender.—Feminine.

Etymology.—The name is derived from the Greek, *meios*, meaning small, in combination with the generic name *Squilla*.

Anchisquilla, new genus

Diagnosis.—Eye of moderate size, cornea bilobed, noticeably wider than stalk (Fig. 4, e, f); ocular scales separate; carinae of carapace reduced, median carina present or absent, posterolateral margin rounded; mandibular palp present or absent; 4 epipods present; dactylus of raptorial claw with 4-6 teeth, upper margin of propodus evenly pectinate; lateral processes of fifth, sixth and seventh thoracic somites single, fifth usually a curved spine (Fig. 6, a); carinae of abdomen reduced or augmented by supplementary carinae; telson with or without supplementary dorsal ornamentation, submedian teeth with movable apices (Fig. 8, b), prelateral lobes present or absent; inner margin of basal prolongation of uropod with or without spines (Fig. 9, b).

Remarks.—*Anchisquilla* includes the following four species of uncertain position:

1. **Squilla fasciata* de Haan, 1844
2. **Squilla miles* Hess, 1865
3. **Squilla mcneilli* Stephenson, 1952
4. **Squilla inermis* Manning, 1965

The species assigned to this genus are probably not closely related to each other, and none shows any great resemblance to any of the other genera recognized herein. The presence of movable apices on the submedian teeth of the telson and the presence of four epipods are the only features that link them together. *A. miles*, in which the eyes (Fig. 4, f) are similar to those found in *Parasquilla* and *Manningia*, with the outer margin longer than the inner, possibly belongs in a new genus. *A. fasciata* resembles *Meiosquilla* to some extent, but has six teeth on the claw, a mandibular palp, and prelateral lobes on the telson. *A. mcneilli* also has a

palp, lacks inner spines on the basal prolongation of the uropod, and differs from the other species in having a median carina on the abdomen and in having the ventral spines of the fifth abdominal somite completely suppressed. *A. inermis* resembles some species of *Clorida*, but differs in having separate ocular scales and in totally lacking dorsal sculpture on the telson. Further study may indicate that each of the species in *Anchi-squilla* should be placed in a separate genus.

Range.—Indo-West Pacific.

Type-species.—*Squilla fasciata* de Haan, 1844.

Gender.—Feminine.

Etymology.—The name is derived from the Greek, *Anchi*, meaning near, in combination with the generic name *Squilla*.

***Cloridopsis*, new genus**

Diagnosis.—Eye small, stalk dilated or margins subparallel, cornea slightly broader than stalk (Fig. 4, g); ocular scales separate; carapace strongly narrowed anteriorly with normal complement of carinae, posterolateral margins evenly rounded; mandibular palp present or absent; 2-3 epipods present; dactylus of raptorial claw with 5-6 teeth; upper margin of propodus pectinate; lateral processes of fifth, sixth and seventh thoracic somites single, process of fifth somite a broad, curved spine (Fig. 6, b); abdomen with normal complement of carinae; telson broad, inflated, dorsal surface smooth, submedian teeth with fixed apices (Fig. 8, c), prelateral lobes present; inner margin of basal prolongation of uropod at most tuberculate.

Remarks.—*Cloridopsis* includes the following species:

1. **Squilla scorpio* Latreille, 1825
2. **Squilla dubia* H. Milne-Edwards, 1837
3. **Squilla gibba* Nobili, 1903
4. **Squilla immaculata* Kemp, 1913
5. *Squilla bengalensis* Tiwari & Biswas, 1952
6. *Squilla terrareginensis* Stephenson, 1953

Cloridopsis most closely resembles *Clorida*, but differs in having separate ocular scales, larger eyes, with the stalk rarely broader than the cornea, and in lacking the movable apices on the submedian teeth of the telson. In addition, the species of *Cloridopsis* lack the dorsal ornamentation of the telson characteristic of most species of *Clorida*.

Range.—Western Atlantic, eastern Pacific, Indo-West Pacific.

Type-species.—*Squilla scorpio* Latreille, 1825.

Gender.—Masculine.

Etymology.—The name is derived from the Greek, *-opsis*, meaning like, in combination with the generic name *Clorida*.

Squilla Fabricius, 1787

Squilla Fabricius, 1787: 333.—Holthuis & Manning, in press (other references).

Diagnosis.—Eye moderate to large, cornea bilobed, broader than stalk (Fig. 5, a); ocular scales separate; carapace narrowed anteriorly, with normal complement of carinae (1 median, 2 intermediates, laterals, and marginals), posterolateral margins with anterior angle; mandibular palp present or absent; 4-5 epipods present; dactylus of raptorial claw with 5-7 (usually 6) teeth, upper margin of propodus evenly pectinate; lateral process of fifth thoracic somite a single spine, lateral processes of next two somites bilobed or single, if bilobed anterior lobe usually small (Fig. 7, a, b); abdomen with normal complement of carinae (paired submedians, intermediates, laterals, and marginals); telson smooth or with dorsal carinae, submedian teeth with fixed apices; prelateral lobes present or absent; inner spine of basal prolongation of uropod with tubercles or erect spines on inner margin.

Remarks.—*Squilla* is restricted herein to the following species:

1. **Cancer mantis* Linnaeus, 1758
2. **Squilla empusa* Say, 1818
3. **Squilla neglecta* Gibbes, 1850
4. **Squilla prasinolineata* Dana, 1852
5. **Squilla biformis* Bigelow, 1891
6. **Squilla panamensis* Bigelow, 1891
7. **Squilla parva* Bigelow, 1891
8. **Squilla aculeata* Bigelow, 1893
9. **Squilla intermedia* Bigelow, 1893
10. **Squilla mantoidea* Bigelow, 1893
11. **Squilla rugosa* Bigelow, 1893
12. **Squilla brasiliensis* Calman, 1917
13. **Chloridella edentata* Lunz, 1937
14. **Chloridella heptacantha* Chace, 1939
15. **Squilla bigelowi* Schmitt, 1940
16. **Squilla hancocki* Schmitt, 1940
17. **Squilla tiburonensis* Schmitt, 1940
18. **Squilla calmani* Holthuis, 1959 (= *S. africana* Calman, 1916)
19. **Squilla lijdingi* Holthuis, 1959
20. **Squilla obtusa* Holthuis, 1959
21. **Squilla surinamica* Holthuis, 1959
22. **Squilla intermedia*: Ingle, 1960
23. **Squilla chydæa* Manning, 1962
24. **Squilla discors* Manning, 1962

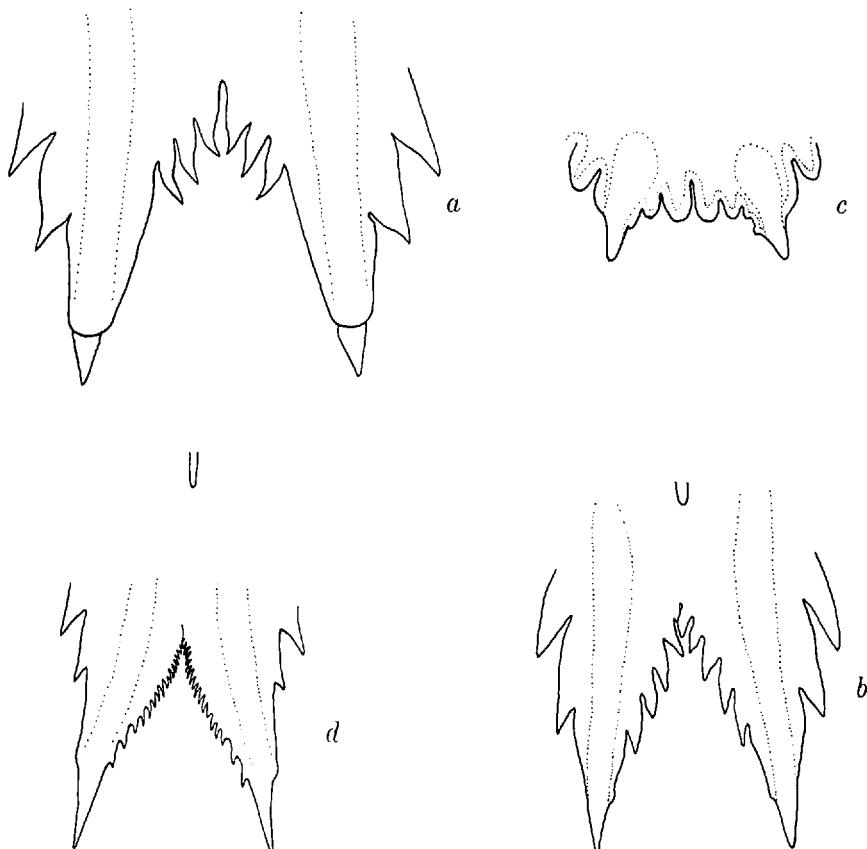


FIGURE 8. Outline of submedian teeth and denticles of telson of: *a*, *Meio-squilla desmarestii* (Risso); *b*, *Anchisquilla fasciata* (de Haan); *c*, *Cloridopsis scorpio* (Latreille); *d*, *Squilloides leptosquilla* (Brooks).

In addition to these 24 species now in the literature, three undescribed species are known to occur in the western Atlantic; these will be described in the forthcoming study of the western Atlantic stomatopods.

The genus *Squilla*, as restricted here, includes moderate to large species with large eyes, well-developed body carination, a single lateral spine on the fifth thoracic somite, and fixed apices on the submedian teeth of the telson. *Oratosquilla*, the Indo-West Pacific counterpart of *Squilla*, always has a bilobed lateral process on the fifth thoracic somite.

Range.—Atlanto-East Pacific.

Type-species.—*Cancer mantis* Linnaeus, 1758, by subsequent designation by Latreille, 1810, p. 422.

Squilloides, new genus

Diagnosis.—Eye of moderate size, cornea bilobed, noticeably wider than stalk (Fig. 5, b); ocular scales separate; carinae of carapace reduced, median carina present or absent, posterolateral margin of carapace usually rounded; mandibular palp present or absent; 4 epipods present; dactylus of raptorial claw with 4-6 teeth, upper margin of propodus evenly pectinate; lateral processes of fifth, sixth and seventh thoracic somites single, process of fifth somite usually a curved spine (Fig. 6, c); carinae of abdomen reduced or normal complement present; telson without supplementary dorsal ornamentation, submedian teeth with fixed apices (Fig. 8, d), prelateral lobes absent; inner margin of basal prolongation with spines (Fig. 9, c).

Remarks.—*Squilloides* includes the following five species:

1. **Squilla lata* Brooks, 1886
2. **Squilla leptosquilla* Brooks, 1886
3. *Squilla tenuispinis* Wood-Mason, 1891
4. *Squilla minor* Jurich, 1904
5. **Squilla gilesi* Kemp, 1911

Squilloides is the Indo-West Pacific counterpart of *Meiosquilla*; *S. leptosquilla* and *S. tenuispinis* in particular resemble the species now placed in *Meiosquilla*, differing chiefly in having a median carina on the carapace and in having the apices of the submedian telson fixed. The other three species of *Squilloides* differ in having six teeth on the claw, a mandibular palp, and in lacking the median carina of the carapace. The two groups of species in this genus should perhaps be referred to two subgenera.

Range.—Indo-West Pacific.

Type-species.—*Squilla leptosquilla* Brooks, 1886.

Gender.—Masculine.

Etymology.—The name is derived from the Greek, *-oides*, meaning like, and the generic name *Squilla*.

Dictyosquilla, new genus

Diagnosis.—Eye very small, cornea not as wide as swollen stalk (Fig. 5, c); ocular scales separate; body completely covered with irregular, raised carinae forming mesh-like reticulation (Fig. 10); mandibular palp present; 4 epipods present; dactylus of claw with 6 teeth, upper margin of propodus fully pectinate; lateral processes of fifth, sixth and seventh thoracic somites bilobed (Fig. 6, d); submedian teeth of telson with fixed apices, prelateral lobes absent; basal prolongation of uropod serrate on inner margin.

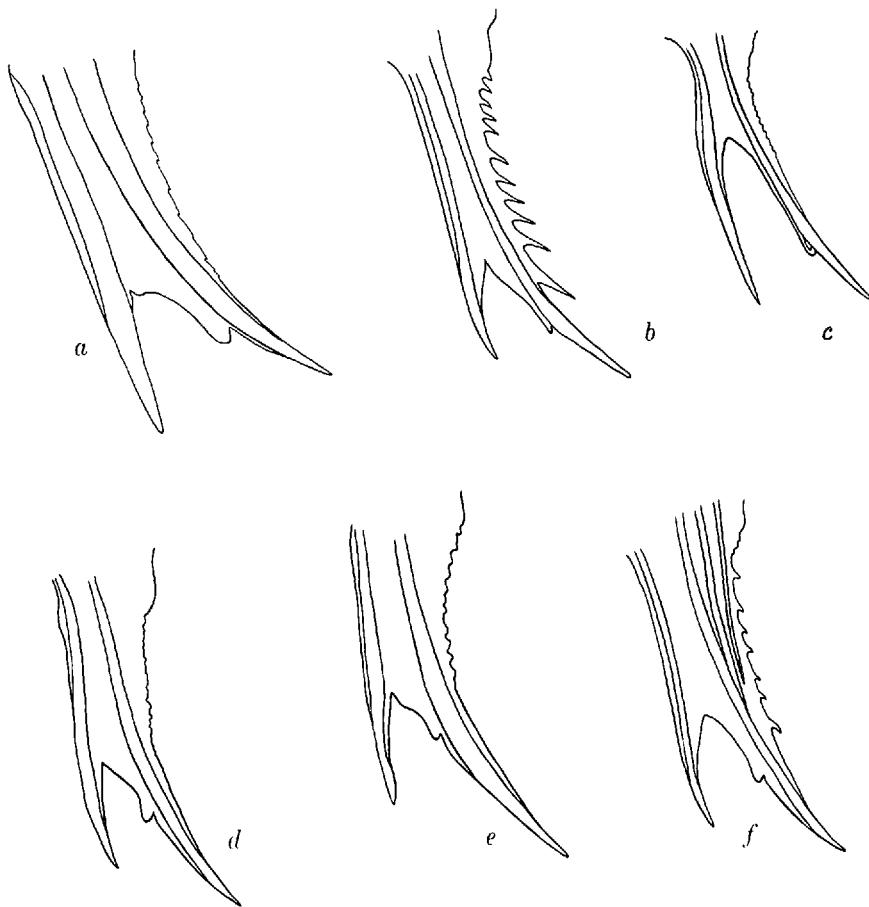


FIGURE 9. Basal prolongation of uropod of: *a*, *Meiosquilla desmarestii* (Risso); *b*, *Anchisquilla fasciata* (de Haan); *c*, *Squilloides leptosquilla* (Brooks); *d*, *Lophosquilla costata* (de Haan); *e*, *Oratosquilla oratoria* (de Haan); *f*, *Carinosquilla multicarinata* (White).

Remarks.—*Dictyosquilla* includes only the following species:

1. **Squilla foveolata* Wood-Mason, 1895

The *Clorida*-like eyes and the intricate pattern of ornamentation on the body of the single species assigned to this genus will immediately distinguish it from any of the other genera with six teeth on the claw and bilobed lateral processes on the sixth and seventh thoracic somites. In this latter feature, *D. foveolata* resembles *Oratosquilla gonyptetes* and the other species of that genus with five teeth on the raptorial claw.

Range.—Indo-West Pacific.

Type-species.—*Squilla foveolata* Wood-Mason, 1895, by monotypy.

Gender.—Feminine.

Etymology.—The name is derived from the Greek, *diktyon*, meaning net, in combination with the generic name *Squilla*.

Lophosquilla, new genus

Diagnosis.—Eye of moderate size, cornea bilobed, distinctly wider than stalk (Fig. 5, d); ocular scales separate; carapace with supplementary short carinae in addition to normal complement; mandibular palp absent; 4 epipods present; dactylus of raptorial claw with 6-7 teeth, upper margin of propodus evenly pectinate; lateral processes of fifth, sixth and seventh thoracic somites bilobed (Fig. 6, e); abdomen with supplementary carinae in addition to normal complement; telson flattened, with supplementary dorsal ornamentation, submedian teeth with fixed apices, prelateral lobes present or absent; basal prolongation of uropod with inner margin serrate (Fig. 9, d).

Remarks.—*Lophosquilla* includes but two species:

1. **Squilla costata* de Haan, 1844
2. **Squilla* sp. prox. *costata* Tiwari & Biswas, 1952

Lophosquilla resembles *Carinosquilla* in some respects, particularly in the reticulate dorsal pattern of ornamentation, but differs in having the lateral processes of the sixth and seventh thoracic somites strongly bilobed and the inner margin of the basal prolongation of the uropod unarmed. In my opinion, the resemblance between *Lophosquilla* and *Carinosquilla* is superficial, and the species in these two genera have independently acquired their body ornamentation.

Range.—Indo-West Pacific.

Type-species.—*Squilla costata* de Haan, 1844.

Gender.—Feminine.

Etymology.—The name is derived from the Greek, *lophos*, meaning crest, and the generic name *Squilla*.

Oratosquilla, new genus

Diagnosis.—Eye large, cornea bilobed, noticeably broader than stalk (Fig. 5, e); ocular scales separate; carapace with normal complement of carinae, rounded posterolaterally or with slight anterior angular prominence; mandibular palp usually present; 4 epipods present; dactylus of raptorial claw with 5 or more teeth (usually 6), upper margin of propodus pectinate

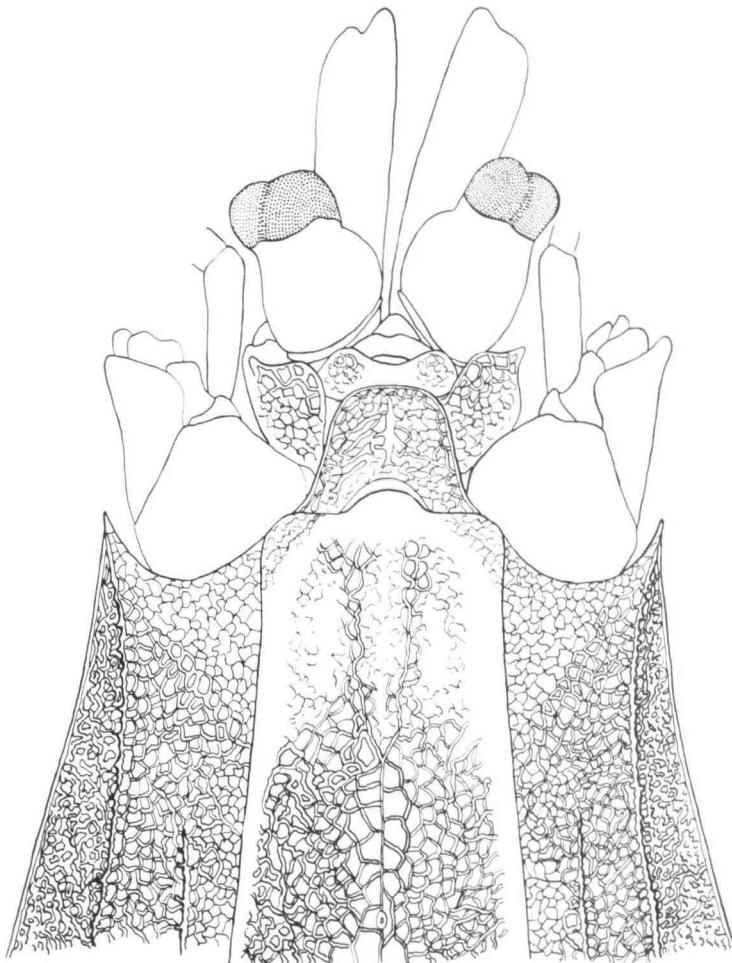


FIGURE 10. Anterior portion of body of *Dictyosquilla foveolata* (Wood-Mason).

(Fig. 3, b); lateral processes of fifth, sixth, and seventh thoracic somites bilobed (Fig. 7, c, d); abdomen with full complement of carinae, median carina absent; telson flattened, lacking supplementary dorsal ornamentation, submedian teeth with fixed apices; prelateral lobes present; basal prolongation of uropod with inner margin serrate (Fig. 9, e).

Remarks.—*Oratosquilla* includes the following species:

1. **Squilla nepa* Latreille, 1825
2. **Squilla oratoria* de Haan, 1844

3. **Squilla massavensis* Kossmann, 1880
4. **Squilla inornata* Tate, 1883
5. **Squilla quinquedentata* Brooks, 1886
6. **Squilla stridulans* Wood-Mason, 1894
7. **Squilla investigatoris* Lloyd, 1907
8. *Squilla quadraticauda* Fukuda, 1911 (= *S. boops* Kemp, 1911)
9. **Squilla gonyptetes* Kemp, 1911
10. **Squilla holoschista* Kemp, 1911
11. **Squilla interrupta* Kemp, 1911
12. **Squilla perpensa* Kemp, 1911 (= *S. anomala* Tweedie, 1935)
13. **Squilla woodmasoni* Kemp, 1911
14. **Squilla mauritiana* Kemp, 1913
15. **Squilla mikado* Kemp & Chopra, 1921 (= *S. zanzibarica* Chopra, 1939)
16. *Squilla indica* Hansen, 1926
17. **Chloridella kempfi* Schmitt, 1928
18. **Squilla fabricii* Holthuis, 1941
19. **Squilla juxtaoratoria* Ward, 1942
20. **Squilla columnia* Townsley, 1953
21. **Squilla imperialis* Manning, 1965

Oratosquilla includes most of the large, common Indo-West Pacific species of stomatopods formerly assigned to the genus *Squilla*. The large body, large eyes, carapace with normal complement of carinae, and bilobed lateral process on the fifth, sixth, and seventh thoracic somites will serve to distinguish members of this genus.

Although Kemp (1913) indicated that those species with five teeth on the claw, including *O. gonyptetes* (Kemp) and *O. quinquedentata* (Brooks), were distinct from the "oratoria" group in which there are always six teeth on the claw, I can find no other major difference between the two groups. Both are very similar in general facies.

Range.—Indo-West Pacific. One species, *O. massavensis*, has been reported from the Mediterranean (Ingle, 1963).

Type-species.—*Squilla oratoria* de Haan, 1844.

Gender.—Feminine.

Etymology.—The name is derived from the specific name of the type-species, *S. oratoria*, in combination with the generic name *Squilla*.

Carinosquilla, new genus

Diagnosis.—Eye large, cornea bilobed, noticeably broader than stalk (Fig. 5, f); ocular scales separate; carapace with numerous longitudinal carinae; mandibular palp present or absent; 4 epipods present; dactylus of raptorial

claw with 5-6 teeth, upper margin of propodus pectinate; lateral process of fifth thoracic somite bilobed, lateral processes of next 2 somites also bilobed (Fig. 6, f); abdomen and telson with numerous longitudinal carinae; submedian teeth of telson with fixed apices, prelateral lobes present; basal prolongation of uropod with row of spines on inner margin (Fig. 9, f).

Remarks.—*Carinosquilla* includes the following three species:

1. **Squilla multicarinata* White, 1848
2. **Squilla lirata* Kemp & Chopra, 1921
3. **Squilla carinata* Serène, 1950

The species of *Carinosquilla* resemble those in *Lophosquilla* mainly in having the body ornamented with numerous longitudinal carinae. Members of the former genus differ in having much larger eyes and spines on the inner margin of the basal prolongation of the uropod. In addition, the species of *Carinosquilla* have many more body carinae than do those in *Lophosquilla*.

Range.—Indo-West Pacific.

Type-species.—*Squilla multicarinata* White, 1848.

Gender.—Feminine.

Etymology.—The name is derived from the Latin, *carina*, meaning keel, in combination with the generic name *Squilla*.

Alima Leach, 1817

Alima Leach, in Tuckey, 1817, unnumbered plate.

Diagnosis.—Eye large, cornea bilobed, noticeably broader than stalk (Fig. 5, g); ocular scales separate; carapace with normal complement of carinae; mandibular palp present or absent; 4 epipods present; dactylus of raptorial claw with 5-6 teeth, upper margin of propodus pectinate; lateral process of fifth thoracic somite bilobed, lateral processes of next two somites each a single lobe (Fig. 7, e, f); abdomen with normal complement of carinae or with 1 additional; telson elongate, supplementary dorsal carinae present or absent, submedian teeth with fixed apices; prelateral lobes present; inner margin of basal prolongation of uropod serrate or tuberculate.

Remarks.—*Alima* includes the following nominal species:

1. **Alima hyalina* Leach, 1817 (= *Squilla alba* Bigelow, 1893)
2. **Squilla laevis* Hess, 1865
3. *Squilla supplex* Wood-Mason, 1895
4. **Squilla hieroglyphica* Kemp, 1911
5. **Squilla hildebrandi* Schmitt, 1940
6. **Squilla labadiensis* Ingle, 1960

Alima, as defined herein, includes small or moderately sized species with a flattened body and the characteristic facies of many Indo-West Pacific species, the bilobed lateral process of the fifth thoracic somite. In general, the posterior lobe of that process is rounded in *Alima*, and the lateral processes of the next two somites are not conspicuously bilobed.

Squilla supplex Wood-Mason, from India, is tentatively assigned to this genus. It differs from all of the other species in the genus in having a mandibular palp and a median carina on the first five abdominal somites. In other features it seems to resemble the other three species closely.

Squilla laevis Hess, from Australia, is the only species in the genus in which the median carina of the carapace is provided with a well-marked anterior bifurcation. In other respects, it closely resembles *A. hyalina* and *A. hieroglyphica*.

It is with some reservations that I use Leach's name for this genus, for the term *alima* has been in use for many years as a category name for a kind of stomatopod larva. However, Leach's name is available and would have to be suppressed through the plenary powers of the Commission before another name could be proposed. There is little justification for burdening the Commission with such a request.

Range.—Indo-West Pacific, Atlantic.

Type-species.—*Alima hyalina* Leach, 1817, by monotypy.

Family Gonodactylidae Giesbrecht, 1910

Gonodactylinae Giesbrecht, 1910: 148.—Gurney, 1946: 134.—Manning, 1963: 325.

Gonodactylidae Manning, 1967: 238 (key).

Definition.—Propodi of third and fourth thoracic appendages longer than broad, lacking ventral ribbing (Fig. 2, g-i); telson (Fig. 1, d) with distinct median carina; submedian marginal teeth of telson always with movable apices, submedian denticles present or absent; no more than 2 intermediate denticles present.

Type-genus.—*Gonodactylus* Berthold, 1827.

Number of genera.—Thirteen, distinguished in key below.

Remarks.—The genera assigned to this family fall into two broad groups, one "centered" around *Gonodactylus* and the other around *Pseudosquilla*. *Gonodactylus* and its allies, *Protosquilla*, *Mesacturus*, *Hoplosquilla*, *Odontodactylus*, and *Hemisquilla*, are morphologically very similar. In all but *Odontodactylus*, the dactylus of the raptorial claw is unarmed; in all but *Hemisquilla*, the ischiomeral articulation of the raptorial claw is distal to the proximal end of the merus. *Hemisquilla* actually shows affinities to both groups of genera, but morphologically it most closely resembles

Gonodactylus and *Odontodactylus*. In all of the genera related to *Gonodactylus*, the portion of the claw proximal to the articulation of the propodus and dactylus is swollen; the swelling is least developed in *Hemisquilla*. Finally, in all of these genera the pectinations normally found on the upper margin of the raptorial claw are reduced in number and extent; the pectinations are usually replaced by a proximal series of obscure serrations.

The genera that seem related to *Pseudosquilla*, including *Parasquilla* and *Pseudosquillopsis* in one subgroup, and *Eurysquilla*, *Eurysquilloides*, *Manningia*, and *Coronidopsis* in another, all have the dactylus armed with teeth, lack the basal swelling on the dactylus, and have a normal or terminal ischiomeral articulation on the raptorial claw. The first three genera named above include slender species, which usually have a compact, subcylindrical body, and all of which have three teeth on the dactylus of the claw. The second group of four genera includes species which have a loosely articulated, flattened body, and which always have more than three teeth on the claw; species in *Manningia* and *Coronidopsis* have four teeth on the claw, and those in *Eurysquilla* and *Eurysquilloides* have seven or more.

Pseudosquilla and its allies are perhaps more conservative than the members of the group of genera allied to *Gonodactylus*, for the former group contains far fewer species than the latter. *Gonodactylus* and *Protosquilla* each have in excess of 15 species. There are no more than six species in the genera allied to *Pseudosquilla*.

Of all of these genera, *Eurysquilla*, with its flattened, loosely articulated body, bears the most superficial resemblance to some of the lysiosquillid. The slender propodi of the maxillipeds and the median carina on the telson, however, will distinguish species of *Eurysquilla* from members of that family.

Parasquilla is the only genus in this family in which the body is longitudinally carinate as in most species of *Squilla*. This feature apparently developed independently in *Parasquilla* and the squillids, and, in my opinion, is no indication of close relationship. The presence of only two denticles on the telson will distinguish species of *Parasquilla* from those of *Squilla* and its allies, in which there are always four or more denticles.

KEY TO THE GENERA OF THE FAMILY GONODACTYLIDAE

1. Ischiomeral articulation terminal; merus grooved inferiorly throughout its length	2
Ischiomeral articulation subterminal, merus projecting posteriorly beyond articulation; inferior groove on merus incomplete	9
2. Dactylus unarmed; sixth abdominal somite unarmed posteriorly	
----- <i>Hemisquilla</i> Hansen, 1895	
Dactylus with teeth; sixth abdominal somite with armed carinae or with posterior spines	3

3. Outer spine of basal prolongation of uropod longer than or subequal to inner	4
Inner spine of basal prolongation of uropod longer than outer	6
4. Basal prolongation of uropod with 2 spines, inner margin unarmed; carapace without carinae	<i>Pseudosquilla</i> Dana, 1852
Basal prolongation of uropod with 3 spines, proximal smallest, with or without additional spinules on inner margin; carapace with marginal carina present on posterior portion of each lateral plate	5
5. First 5 abdominal somites with prominent carinae; telson with submedian denticles	<i>Parasquilla</i> Manning, 1961
First 5 abdominal somites not carinate; telson lacking submedian denticles	<i>Pseudosquillopsis</i> Serène, 1962
6. Rostral plate with 2 apical spines	<i>Coronidopsis</i> Hansen, 1926
Rostral plate with or without 1 apical spine	7
7. Dactylus of claw with 4 teeth; rostral plate pentagonal	<i>Manningia</i> Serène, 1962
Dactylus of claw with more than 4 teeth; rostral plate variable in shape but not pentagonal	8
8. Antennular somite greatly elongated; telson with submedian denticles	<i>Euryssquilloides</i> Manning, 1963
Antennular somite not elongate; telson without submedian denticles	<i>Euryssquilla</i> Manning, 1963
9. Dactylus of claw with teeth; rostral plate without slender median spine	<i>Odontodactylus</i> Bigelow, 1893
Dactylus of claw unarmed; rostral plate with slender median spine	10
10. Anterolateral angles of carapace anterior to base of rostral plate	11
Anterolateral angles of carapace not anterior to base of rostral plate	12
11. Rostral plate with anterolateral angles rounded or acute; distal spines on uropodal exopod not strongly recurved	<i>Gonodactylus</i> Berthold, 1827
Rostral plate sharply trispinose; distal spines of uropodal exopod strongly recurved	<i>Mesacturus</i> Miers, 1880
12. Mandibular palp present; posterior margin of sixth abdominal somite convex in dorsal view; sixth abdominal somite usually fused with telson	<i>Protosquilla</i> Brooks, 1886
Mandibular palp absent; posterior margin of sixth abdominal somite straight (transverse) in dorsal view; sixth abdominal somite not fused with telson	<i>Hoplosquilla</i> Holthuis, 1964

SUMARIO

REVISION DE LA FAMILIA SQUILLIDAE (CRUSTACEA, STOMATOPODA),
CON LA DESCRIPCION DE OCHO NUEVOS GENEROS

Especies recientemente asignadas al Orden Stomatopoda ha resultado que forman cuatro distintos grupos de géneros y especies que son reconocidos como familias.

La familia Squillidae Latreille, 1803, incluye aquellas especies con maxilípedos delgados, con carina media y más de cuatro dentículos intermedios en el telson y con larvas que incuban como una pseudozoea y se desarrollan en una alima. La familia Squillidae incluye 14 géneros, de los cuales ocho son descritos como nuevos y dos son resucitados de la sinonimia de *Squilla*.

La familia Gonodactylidae Giesbrecht, 1910, incluye especies con maxilípedos delegados, con carina media y menos de cuatro dentículos intermedios en el telson y con larvas que incuban como una pseudozoea y se desarrollan en una erichtus. Trece géneros, ninguno nuevo, se asignan a esta familia.

La familia Lysiosquillidae Giesbrecht, 1910, incluye especies con maxilípedos gruesos, sin carina media en el telson y con larvas que se incuban como antizoea. Nueve géneros, ninguno nuevo, son colocados en esta familia.

La familia Bathysquillidae Manning, 1967, incluye un género en el cual los maxilípedos son delgados y el telson está provisto con carina media y cuatro pares de dientes marginales, cada uno de los cuales tiene un ápice móvil. Se desconocen sus larvas.

Se ilustran los caracteres para el diagnóstico de cada género de Squillidae, así como alguno de los caracteres usados para distinguir las familias. Se presentan claves para las familias y para los géneros en cada familia.

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